Habitat Correlates of the Siskiyou Mountains Salamander, *Plethodon stormi* (Caudata: Plethodontidae); with Comments on the Species' Range.

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ABSTRACT

A stratified systematic sampling design was used to investigate the habitat relationships of the Siskiyou Mountains salamander (*Plethodon stormi*) in southwestern Oregon and northwestern California. We sampled 239 sites, 163 north and 76 south of the Siskiyou crest. Each site was within at least 5-7 ha of relatively homogeneous forest or post-forest habitat, where we measured 128 characteristics of the environment. Variables included attributes at the landscape, macrohabitat, and microhabitat scales. Salamander sampling consisted of area-constrained sampling of 7x7 meter plots with at least 25 % rock cover at each site. Subsets of 117 (Oregon) and 92 (California) variables were used in hierarchical analysis of habitat associations using discriminant analyses and regression. The most consistent predictors of salamander presence across scales were those variables that modeled climatic factors. Overall, our results indicated a significant association of the Siskiyou Mountains salamander with conditions found in older, undisturbed forests with a closed canopy, moist microclimate, and rocky substrates dominated by cobble-sized pieces. These habitat attributes appear optimal for reproductive success and long-term survival throughout the range of this species. The Siskiyou Mountains salamander may require those ecological conditions found primarily in late seral forests.

INTRODUCTION

The Siskiyou Mountains salamander (*Plethodon stormi;* PLST) is currently a California State Threatened species and is listed as Sensitive (critical) by the state of Oregon. In 1994, PLST was one of five amphibians identified as a species requiring specific habitat protections by the USDA Forest Service in the Record of Decision for the Final Supplemental Environmental Impact Statement for Management of Habitat for Late-successional and Old-growth Forest Related Species Within the Range of the Northern Spotted Owl (USDA et al. 1994). Development of strategies for management and conservation of this species required a more thorough investigation of environmental requirements and the extent of its range, with particular interest in those habitat elements and areas most likely affected by future land management.

Little information is available regarding environmental requirements and habitat use of the Siskiyou Mountains salamander. The majority of past studies have focused efforts on sampling areas expected to yield large numbers of salamanders or on areas requiring status reviews prior to ground disturbing projects. Previous knowledge of the species' niche stemmed from surveys within the Applegate Valley of Oregon and Seiad Valley of northern California, which looked at only a few stand types and restricted the elevational limits to areas less than 1100 m (490m to 1100m; Highton and Brame 1965, Nussbaum et al. 1983). Thus, previous information on the niche of this species is incomplete. For example, Nussbaum et al. (1983) characterized habitat for PLST as stabilized talus in old-growth forest stands with northern exposures. Populations of *P. stormi* have been found in close association with surface rock (Herrington 1988; Nussbaum et al. 1983; Blaustein et al. 1995). Nussbaum et al. (1983) reported that populations of PLST are associated with talus deposits in inland areas where forest floor litter is thin or absent. However, Behler (1979) and Stebbins (1985) concluded that habitat for this species is often blanketed in leaf litter from deciduous trees and with moss.

In the absence of more thorough information on specific habitat associations of the Siskiyou Mountains salamander, management for this species has been based on habitat models derived for a closely related species, the Del Norte salamander (*Plethodon elongatus*). Welsh and Lind (1995) used a range-wide sampling approach designed to determine habitat attributes of the Grinellian niche (James et al. 1984) for *P. elongatus.* Here we have taken the same approach with the Siskiyou Mountains salamander which occupies forests in Oregon and California with environmental conditions similar to those that support *P. elongatus.*

Plethodon stormi is a completely terrestrial member of the family Plethodontidae. As such, this species is lungless, with all respiration occurring through its moist skin. Feder (1983) describes the physiological limitations that constrain a species like PLST in the following way: "temperate zone, lungless salamanders are limited to microclimates that provide high relative humidity and relatively low temperatures. The skin must be moist and permeable for gas exchange to take place." Plethodontid salamanders lose water when outside burrows and retreats, even in moist microhabitats. To restrict water loss, these species may limit surface activity for foraging and courtship to all but very wet periods. They remain under surface cover objects during the day and are active at night. Plethodontid salamanders are primarily "sit and wait" predators which forage primarily on small invertebrate prey on the forest floor or beneath cover objects at night. It is likely that they also opportunistically feed under cover objects during the day (for references on the natural history of plethodontid salamanders see citations in Welsh and Droege 2001).

In addition to a paucity of data on the habitat associations of *P. stormi*, information on the range of this species is incomplete. Historic accounts reported the Siskiyou Mountains salamander only from the upper Applegate River drainage in southern Oregon and from the Seiad Creek drainage east to the Horse Creek drainage in northern California. These early estimates restricted the species range to an area of 160.9 sq. km. As a result of recent survey efforts associated with Survey and Manage provisions of the Northwest Forest Plan (Clayton et al. 1999), the known range has been expanded. However, the focus of those surveys was to identify occupied sites in proposed project areas prior to ground-disturbing activities, not to examine range extent. Consequently, our second objective was to collect new information on the distribution of *Plethodon stormi*. The species is presently known to exist in Jackson and Josephine counties in Oregon and northwestern Siskiyou County, California. The Del Norte salamander, as it is currently defined by systematists, occupies a broader geographic range, one that is located primarily to the west of the areas occupied by the Siskiyou Mountains salamander, but also extends further north and south. The Del Norte salamander is also known from Humboldt, Trinity and Del Norte counties in California and Coos, Curry, and Douglas counties of Oregon. The two species' ranges abut each other in western Siskiyou County in California and in Josephine County in Oregon. Until information on the entire range of *P. stormi* exists, land management that accommodates this species will be limited, and outlier populations, possibly some with unique genetic attributes, may be lost. With these concerns in mind, the objectives of this study were to: (1) investigate and elucidate the environmental relationships of *P. stormi*, including aspects of stand structure and composition, and (2) investigate, the limits of the species' geographic range.

MATERIALS AND METHODS

Site Selection

Initial sampling took place within the known range of the species as described by historic accounts (Highton and Brame 1965, Nussbaum et al. 1983, Stebbins 1985, Herrington 1988, Behler and King 1979, Leonard et al. 1993, Brodie 1970, Bury 1973). Additional localities were discovered as a result of the survey protocol requirement that all potential habitats with in a 25 mi radius of known sites on federal lands be surveyed prior to ground-disturbing activities (Clayton et al. 1999). A recent new locality record within the Grider Creek drainage extended the southwestern boundary of the range to encompass some areas south of the Klamath River (S. Cuenca, pers. comm.). As other range extensions were discovered and made known to us, sampling was expanded to include these new drainages.

In the past, the upper elevational limit for the species was reported to be 1100 m (3600 ft) above sea level (Nussbaum 1974, Nussbaum et al. 1983; Stebbins 1985). In spring 1994, PLST were found by D. Clayton at sites along the Siskiyou Crest separating Oregon from California, and seven of these sites were above 1100 m in elevation. An occupied site was discovered at 1494 m elevation on Fruit Growers Supply Company lands. (D. Miglaw, pers. comm.) These new localities indicated that more information was needed on the elevational limit for this species. Consequently, selection of our sampling areas was not restricted by elevational considerations.

In order to distribute sampling across the range of the Siskiyou Mountains salamander in Oregon and California, and thus derive results with the broadest possible application, sites were chosen using a stratified systematic design with a random component at four nested levels: (1)

biogeographic; (2) U. S. Geological Survey (USGS) township, range and section; (3) seral stage; and (4) minimum essential microhabitat. These levels are described in detail below. A stratified random sampling design was chosen to be the most efficient, cost-effective method of site placement. Stratification allows sampling to be dispersed equally along particular environmental gradients, insuring a full range of possible values for the variables of interest. This method also insures a relatively equal sampling effort across the range of the species and the variety of habitat types available within that range.

The first level of sampling (biogeographic) spanned the entire range of the species, without limits on elevation, parent geology or vegetation type. All sample sites occurred within the drainages of the Klamath, Scott and Upper Applegate rivers on public and private lands (Figure 1).

The second level of sampling (township and section) provided a framework within which sites were selected randomly across the species' range. This level of selection is based on the USGS township and range system, wherein each quadrangle is comprised of 36 one square mile sections (in most areas). Due to the small range of this species and to insure adequate sample sizes, all of the townships within the species' range were sampled. Within each township, four random sections were chosen. Sections that contained large areas that were inaccessible, such as roadless, wilderness areas that required more than a day hike to access, were replaced by selecting another random section. These relatively inaccessible areas were omitted from the study because of logistic constraints. Sections that lacked the appropriate microhabitat (see below) were also replaced by other sections. In this case, the replacement was randomly chosen from the eight sections that adjoined the original section.

The third level of sampling (seral stage) focused on sites from across the entire forest seral

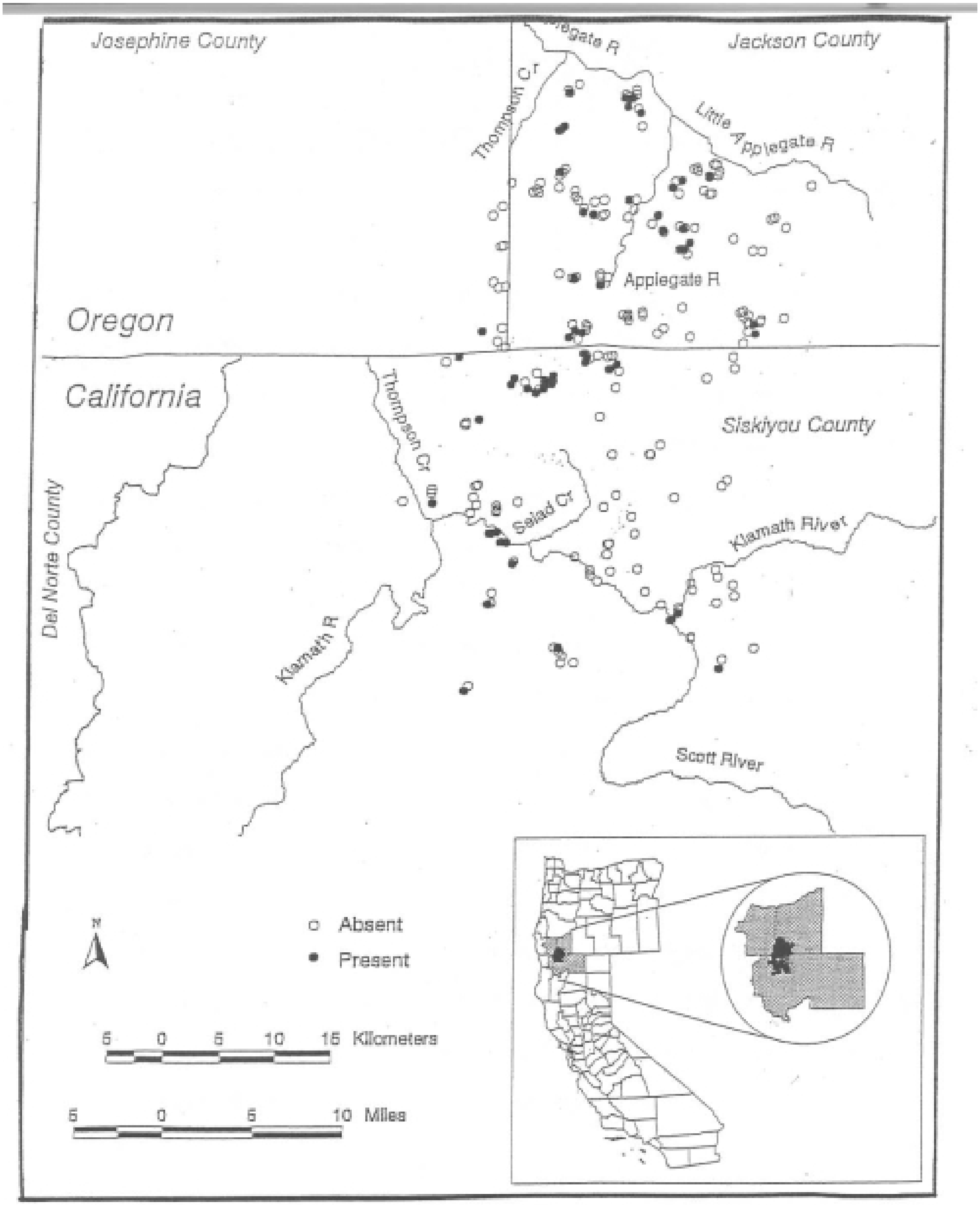


Figure 1. Geographic relationships of sites sampled for the Siskiyou Mountains salamander, *Plethodon stormi*, in Josephine and Jackson counties, Oregon and Siskiyou County, California. All sites are located within the known range of the species. Sampling occurred in the fall and spring 1995 to 1998. Solid circles represent sites with salamanders present (n = 64); open circles represent sites lacking salamander detections (n = 163).

continuum found within the species' range. Within each section up to four sites were located, where possible, one in each of four possible stages: pre-canopy or clear cut (0-30 yrs), young forest (31-99 yrs), mature (100-199 yrs), and old-growth (200 +yrs) (Franklin et al. 1986, Franklin and Spies 1991). Sampling plots were located in stands at least 5-7 ha (12.4 - 17.3 ac) in size that were relatively uniform in tree species composition and tree size class distribution. Potential stands were located using aerial photos and vegetation maps. At this level, where possible, more than one potential stand in each seral stage was selected within each section. Stand visits were then necessary to assess the suitability of potential sampling plots within stands using the criterion presence of appropriate microhabitat (see below). Sites on managed lands were not selected if disturbance had occurred within two years of our sampling. Data from sites with recent disturbance would likely have described the salamanders' response to the disturbance and would not have yielded unbiased data on their environmental associations.

Because the variables and study design were selected to best describe homogeneous areas, our study design required that animal sampling plots be surrounded by contiguous forest or pre-canopy vegetation of relatively uniform age, structure and composition. This requirement precluded sampling of transitional areas, such as edges, where forested stands meets recently harvested areas. Sampling such areas would have led to large increases in variability and violations of analysis assumptions. While transitional areas may have contained PLST, such areas will require additional study to determine their effects on the occurrence and abundance of this salamander.

The fourth level of sampling (minimum essential microhabitat) involved the placement of search plots within the stands selected by the above criteria. Final stand selection was based on the minimum essential microhabitat rocky substrate within a given stand. The intent was to maximize time, effort, and the usefulness of the data set. This involved eliminating sites that had little or no possibility of containing detectable PLST because they lacked sufficient surface rock cover to support salamanders. Since the importance of rock type in determining the occurrence of PLST had not been previously investigated, rocky substrates in this study consisted of any rock type, such as chert, slate, shale, or schist, with at least some cobble-size pieces (>64mm in diameter on the shortest axis) on the surface. This insured that at least some rock large enough to provide cover to individual PLST was searched. Once it was determined by visual inspection that a stand contained such substrates, a plot center was established in the area of greatest rock concentration, at least 75 m (246 ft) from any forest edge. Generally, a minimum of 25% of the 7x7 m (23x23 ft) area surrounding the plot center was covered with this rock. Such rock did not have to be completely exposed, and rock covered by leaf litter or other organic debris was easily discerned. We selected the minimum rock cover of 25% based on pilot sampling and previous studies on a closely related species that indicated that >25% rock cover provided sufficient numbers of captures for a robust analysis (Welsh and Lind 1995). While PLST may occur in low densities in areas with less rock cover, we attempted to maximize search effort by limiting it to areas most likely to yield sufficient captures of PLST when present for a robust analysis of their habitat relationships.

<u>Animal sampling</u>

Intensive area-constrained searches (Welsh 1987, Bury and Corn 1990) were conducted during daylight hours. This approach required the thorough search of each 49 m^2 sample area by one or more workers. Each site was systematically searched for adult and juvenile salamanders with all cover objects turned, and finer substrates carefully hand sifted, down to 15 cm. Surface rock deposits with large interstitial spaces and little material filling the spaces tended to make captures more difficult. Detections in this type of habitat were possible with alert field crews, however, escaping individuals were counted. Salamander density was calculated for each site sampled.

This species spends most of the year beneath the surface, presumably in rock deposits, and is active on the surface for limited periods, during spring and fall, when climatic conditions allow. Consequently, sampling times were restricted to periods with suitable microclimatic conditions when surface or near-surface activity was likely. Spring sampling typically occurred in March and April, and fall sampling occurred from September to early November. Assessments of suitable microclimatic conditions for sampling were based on guidelines described in Clayton et al. (1999). The climatic requirements were: (1) sampling only during the appropriate months of the year, (2) sample only when relative humidity of the air at the site was at least 45%, (3) sample only when air temperature was within the range 4-18 °C; and (4) the soil under the first layer of cover was moist to the touch. Since rainfall and other climatic conditions varied by drainage, when possible, nearby reference sites were used to verify surface activity by salamanders. Surface activity in areas near a survey site was determined with a minimum of disturbance to the substrate.

Measuring Biotic and Abiotic Parameters

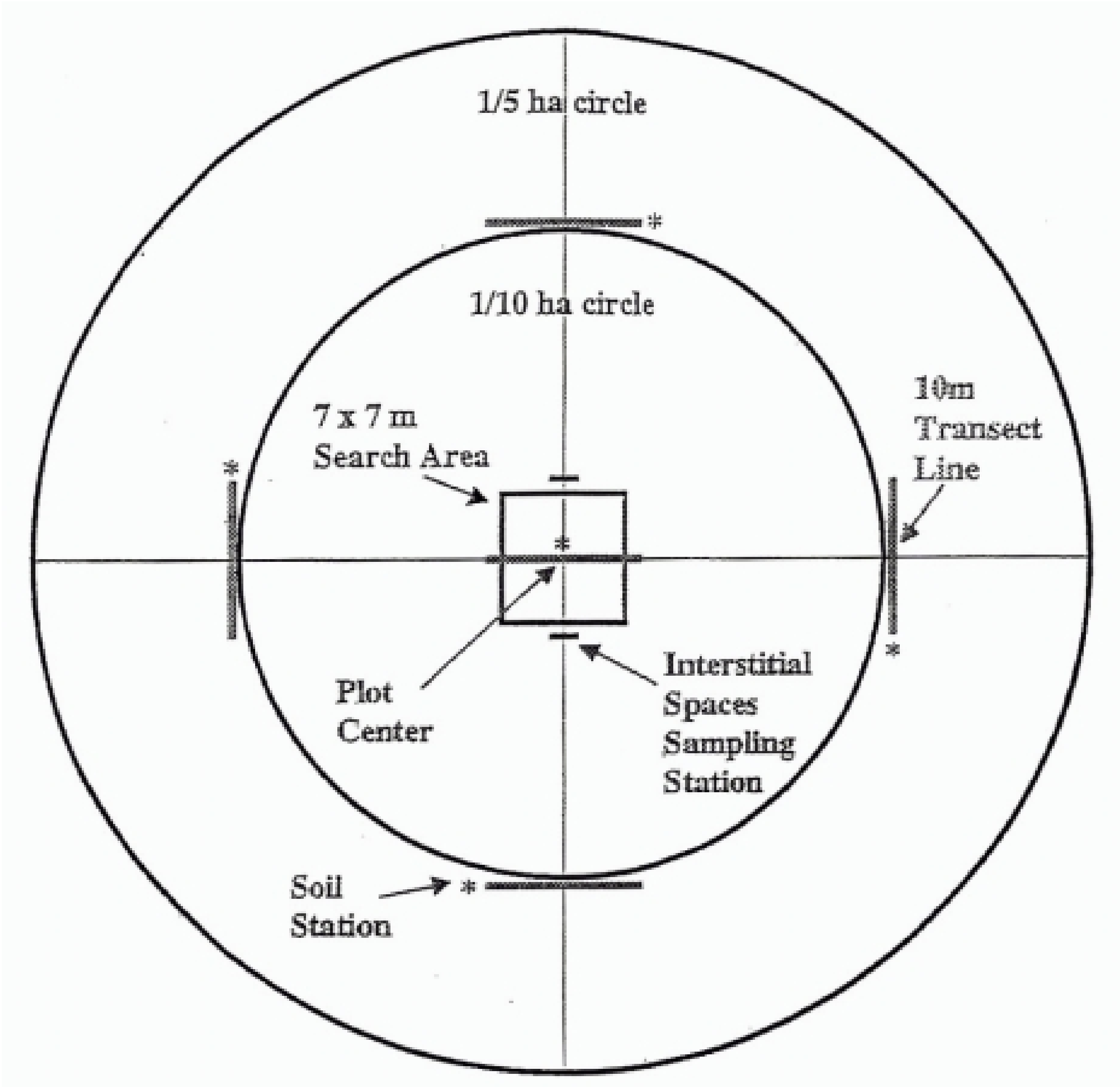
Environmental variables to be sampled were selected using three guiding criteria: (1) parameters that indicate important structural, compositional, and microclimatic aspects of the forest environment important to western plethodontid salamanders, as indicated by previous research (Nussbaum et al. 1983; Stebbins 1985; Herrington 1988; Welsh and Lind 1995, and citations therein); (2) parameters that represented changes in structure and composition of the forest resulting from natural succession or from management practices such as timber harvesting and reforestation, or natural disturbance events such as fire, or landslide; and (3) parameters that incorporated aspects of the forest environment reflecting three spatial scales: landscape, macrohabitat and microhabitat.

Our approach was to measure a wide range of parameters and then eliminate redundant variables prior to statistical analyses. Measurements of course-scale site attributes such as aspect and elevation (landscape scale), forest structure (macrohabitat scale), and microhabitat variables resulted in data collection for 120 continuous independent variables and eight categorical independent variables. See Appendix I for the complete list and details on methods of measurement and Figure 2 for details about data collection. Analyses were performed on the northern and southern portions of the species range in two parallel efforts. The analyses were partitioned based on plot location relative to the Siskiyou Mountains crest (e.g., north or south); this crest roughly follows the Oregon-California border. We determined that these two versants were too different in climate and vegetation to be analyzed together. Additionally the crest may provide a significant barrier to gene flow. Those sites occurring within California, but north of the Siskiyou crest, were included with the Oregon sites in our analyses and in the discussion that follows.

One hundred sixty-three sites were sampled north of the Siskiyou Crest (Oregon sample) and 76 sites were sampled south of the Siskiyou crest (California sample) for a total of 239 sites.

Statistical Analyses

We performed preliminary descriptive analyses to review the distributions of the initial 12.8 variables. Histograms, normal score plots, and measures of skewness and kurtosis (SAS 1990), were used to assess the normality of distributions, and deviations from normality were corrected by appropriate transformations (natural log; square root, or arcsine square root [Zar 1984, Sokal and Rolf 1981]) Reduction of variables prior to analysis was based on elimination of redundancy using correlation analyses. Those variables showing the strongest correlations with salamander numbers



Search area = 7 x 7m (49 m^2)
Inner circle = 1/10 ha (17.8 m diam)
Outer circle = 115 ha (25 m diam)

Figure 2. Diagram of the circular plot design used to sample vegetation and animal sampling, which was used at plots searched for Siskiyou Mountains salamanders from 1995 to 1998.

were retained, and those variables with predominately zero values (>75%) were omitted. This variable reduction method. resulted in sets of 92 variables for the California sites and 117 variables for the Oregon sites (see Appendix II a and b, respectively). In the subsequent multivariate analysis we assumed that univariate normality inferred multivariate normality (Stevens 1986). However, no tests were performed to assess this assumption.

We employed discriminant function analysis (DA) to compare the variation in environmental parameters between sites with salamanders and sites in which salamanders were not detected (hereafter without salamanders). This approach determined the range of environmental attributes which provide conditions suitable for the occurrence of the species.

For multivariate analyses we grouped the independent variables into ecologically meaningful subsets, or ecological components (see Welsh and Lind 1995) based on similarity of spatial scale and vertical stratum. of the forest environment (Appendix II a, b). For those variables that could model relationships at more than one spatial scale, the assignment to a particular scale and ecological component was based on the scale at which the variable was measured (Appendix II, Fig. 2). This approach has practical application for resource managers because these ecological components can be directly related to those aspects of forest structure commonly manipulated or altered during activities such as timber harvesting and road building. Significant variables from each subset of the ecological components analyses were subsequently combined in final analyses to derive composite habitat models that incorporated multiple components and scales.

A two-group DA (SAS 1990) was run for each ecological component using a stepwise procedure to select variables. We tested the null hypothesis that a given habitat variable did not add any additional discriminatory power. Variables entered the model if their P values for the partial F

statistic were ≤0.10. For model building, we chose a moderate significance level (*alpha* = 0.10) because: (1) it permits more variables to enter the models thus providing the best discrimination power for small samples (Constanza and Afifi 1979); (2) a more moderate alpha level reduces the chances of Type II errors; and (3) a moderate alpha level provides a criterion more appropriate for detection of ecological trends (Toft and Shea 1983, Toft 1991). Once the variables were selected, a linear discriminant function was determined on the basis of those variables. Besides the assumption of multivariate normality required for statistical inferences, DA assumes homogeneous variance-covariance structure among groups (Neff and Marcus 1980). Tests for heterogeneity among variance-covariance matrices were performed using Bartlett's modification of the likelihood ratio test (with *alpha* = 0.05; SAS 1990), and we compared results of classification success for both linear and quadratic functions where appropriate. However, we present all results in terms of linear functions because quadratic functions yielded classification results similar to those of the linear functions, linear functions are easier to interpret, and the stepwise technique used to choose variables is linear. Standardized structure coefficients are presented as an indication of the relative contribution of each variable chosen by stepwise DA to the discriminant function (Rencher 1992).

We employed a jackknife procedure (SAS 1990) for the component models and added a re-substitution test (SAS 1990) for the composite models, in order to evaluate the classification success of each. Cohen's Kappa (Thus et al. 1984) was computed for each test to indicate classification success compared with chance alone; the level of acceptable performance was determined using *alpha* = 0.05. In classification tests to assess the performance of the discriminant function models, we assumed that our random systematic site selection yielded a proportion of sites with and without salamanders that reflected the true proportion. Thus, we adjusted the prior probabilities of group membership accordingly (priors proportional) (SAS 1990).

Univariate correlations and single or multiple regression analyses were performed on single and multiple variables, within sample size constraints, that were found to be informative or major contributors to significant models in the DA analyses. Regression analysis determined whether environmental parameters varied with variation in salamander numbers.

RESULTS

We sampled 239 sites between 8 March 1995 and 27 June 1998 (Figure 1), of which 163 sites were north of the Siskiyou crest (Oregon sample) and 76 sites were south of the Siskiyou crest (California sample). The number of sites sampled by stand age, subset by northern and southern samples is reported in Figure 3. Chi-square goodness-of-fit-tests yielded no significant differences from a 1:1:1:1 relationship among the age classes sampled (Figure 3). Thirty percent of the Oregon sites (49) had salamanders, for a total of 137 captures, consisting of 39 juveniles, 26 subadults and 71 adults. One salamander of unknown life stage escaped. Twenty percent of the California sites (15) had salamanders, with a total of 38 captures, including six juveniles, 14 subadults and 17 adults. One salamander of unknown age escaped. Total captures at sites with salamanders ranged 1-13 animals in the 49 m^2 plots (1-13 at northern sites, 1-6 at southern sites). Densities averaged 0.057 salamanders/ m^2 at the Oregon sites and 0.052 salamanders/ m^2 at the California sites.

California Sites

Discriminant Analysis.--The landscape-scale model that best discriminated between sites south of the Siskiyou crest with and without salamanders consisted of latitude, elevation, years since disturbance, and average annual precipitation (Table 1). More sites with salamanders were detected toward the eastern portions of the species' range. These sites were lower in elevation, had greater

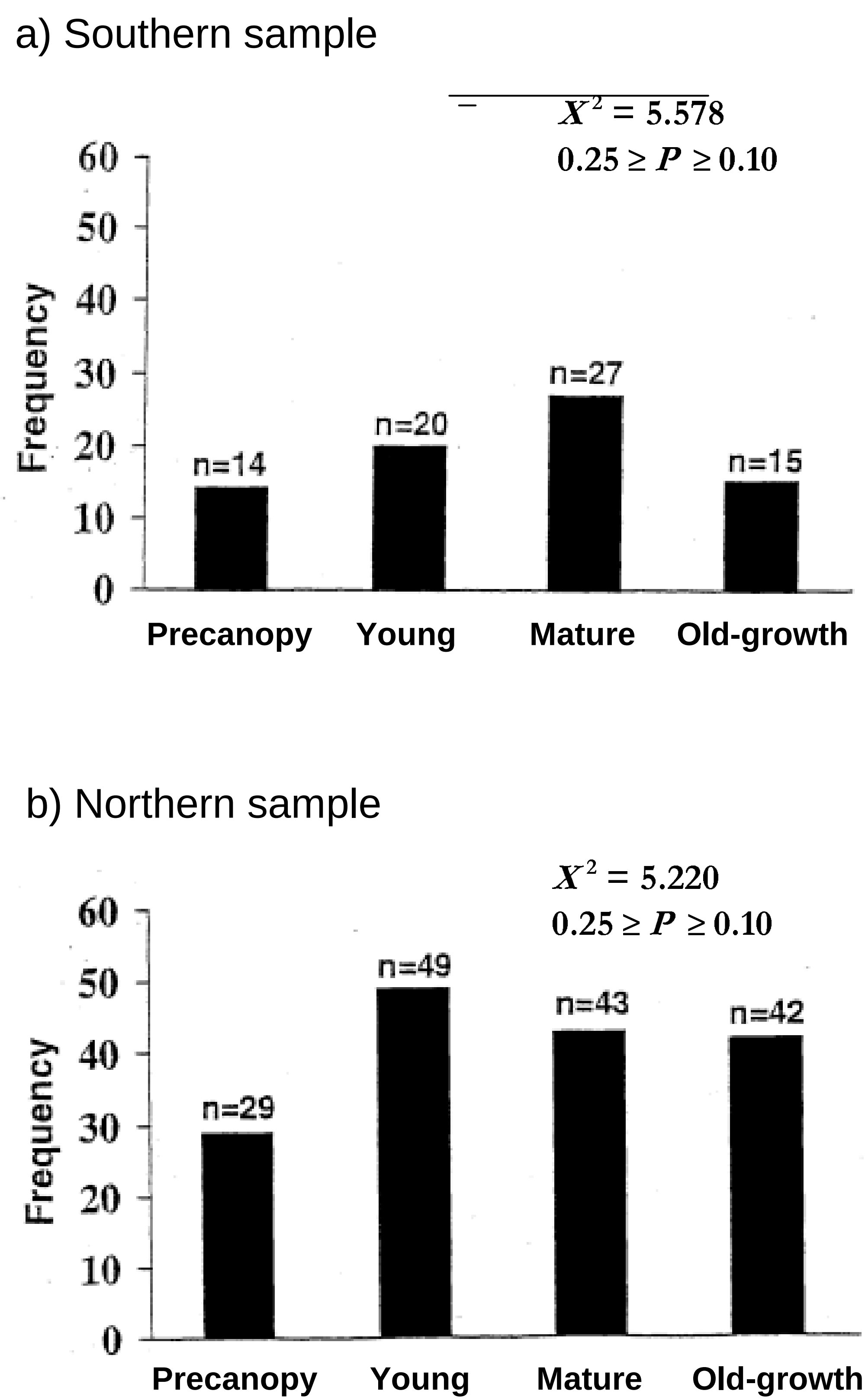


Figure 3. Numbers of plots sampled by forest age class (pre-canopy: 0-30 yrs, young: 31-99, mature: 100-199, old-growth: 200+). The data are split into two groups based on location relative to the Siskiyou Mountains crest; a) south of the crest, b) north of the crest. Chi-square tests were used to test for equal sampling across age classes.

time since disturbance, and had higher mean annual precipitation (Table 1). Annual precipitation across California sites ranged from 58.4 -195.6 cm ($\bar{x}$ =101.6 cm on sites without salamanders; $\bar{x}$ = 122.4 cm sites with salamanders; Appx. III). These amounts were compared to Oregon sites where the more dependable precipitation ranged from 63.5 - 160.0 cm, but the means did not differ for those with and without salamanders ($\bar{x}$ = 92.6 cm on sites without salamanders; $\bar{x}$ = 92.6 cm sites with salamanders; Appendix. III). Sites with captures were associated with annual rainfall totals of > 63.5 cm in California and > 68.6 cm in Oregon. The landscape scale model distinguished between sites and with and without salamanders 80.3% of the time, and 24.4% better than chance (Table 1).

Four of the seven macrohabitat-scale ecological components (Appendix. IIa) produced significant models (Table 1). The tree model consisted of one variable, minimum Douglas-fir diameter at breast height, indicating a minimum size threshold for this conifer may be important at sites that supported salamanders (Table 1). The dead and downed wood component also yielded a single variable model, small decayed conifer logs; sites with salamanders tended to have more small decayed conifer logs than those without salamanders (Table 1). The ground cover component model indicated that sites with salamanders had more rock cover present, but less of it was gravel-sized than on sites without salamanders (Table 1). The forest climate model indicated that sites with salamanders had lower levels of solar radiation, higher canopy closure, and higher subsurface soil temperatures than sites without salamanders. All four significant macrohabitat-scale models had 80% or better site classification success, but only two performed better than chance (Table 1).

Four of the six microhabitat-scale components yielded significant models, which described more boulders, deeper leaf litter, higher canopy closure, higher subsurface soil temperatures at plot

Table 1. Results of our two-group stepwise discriminant analyses of 76 sites[1] sampled for the Siskiyou Mountains salamander (*Plethodon stormi*) south of the Siskiyou Mountains crest (California). Independent variables were grouped for separate analyses by ecological component (Appendix II a). Models were tested for classification success (% correct) with a jackknife procedure; P values indicate the significance of each model; and Cohen's Kappa statistic (Thus et al., 1984) indicated its success relative to chance alone.

Scale	Model variable(s)	Model jackknife score		Cohen's Kappa	Mean greater for sites with salamanders
		%	*P*		
Landscape:	Latitude	80.26	0.0013	0.2440	no
	Elevation				no
	Years since disturbance				yes
	Average annual Precipitation				yes
Macrohabitat:	Minimum Douglas-fir diam.*	80.26	0.0395	-0.0253	yes
	Sm. decayed conifer logs*	80.00	0.0393	0.1124	yes
	Rock_L[2]	80.00	0.0317	0.1949	yes
	Gravel_V[2]				no
	Solar index	81.33	0.0041	2.64×10^{-16}	no
	Minimum % canopy closed (stand)				yes
	Average subsurface soil temp.				yes

[1] Missing values for 1 site resulted in a sample size of 75 for the calculations of macrohabitat scale models; 3 sites were missing data in the forest climate component resulting in a sample size of 73.
[2] L = proportion of transect line, V = visual estimate (%) 1/10 ha circle, AV = visual estimate (%) of salamander search area.
* Indicates a model with heterogeneous variance-covariance matrices.

Table 1. (continued)

Microhabitat:	Bracken Ferns_L8	80.26	0.0378	$2.64x10^{-16}$	no
	Leaf litter_AV [2,*]	80.26	0.0451	$2.64x10^{-16}$	yes
	Boulder_AV	80.26	0.0341	$2.64x10^{-16}$	yes
	% Canopy closed (plot center)	78.67	0.0485	-0.0487	yes
	Subsurface soil temperature (plot center)				yes

centers, and lower Bracken fern cover on sites with salamanders compared to sites without (Table 1). While these microhabitat scale models had classification success > 78%, none performed better than chance (Table 1).

The final composite discriminant analysis provided a means to evaluate the relative importance of those variables that determine presence/absence as derived from the individual component analyses. The composite DA model, derived from five ecological components, had variables which entered in the following order: subsurface soil temperature, annual precipitation, years since disturbance, % canopy closed (measured at plot center), small decayed conifer logs, and rock cover (Table 2). This model had a classification success of 80.6 %, 25.3% better than chance and a resubstitution success of 87.5%, 44.6% better than chance (Table 2).

Scatter Plots arid Regression Analyses. --These analyses determine which environmental parameters varied with changes in salamander numbers. The stand scale minimum canopy closure resulted in a scatter plot pattern that indicated, with the exception of one site, that the minimum canopy closure at occupied sites was 45% (Fig. 4a). Average canopy closure showed a similar pattern, with sites occupied by salamanders having not less than 70% closed canopy ($\bar{x}$ = 80.6%; 95% confidence interval, 68.0-93.3%) (Fig. 5a). The strong relationship between forest canopy and stable within-stand microclimate (see Chen et al. 1999) may also contribute to the highly significant relationship we found between salamander density and soil temperature at the surface. Sites with salamanders captured at or near the surface had a fairly narrow soil temperature range from 5-16 °C (R^2 =0.38; Fig. 6a).

Table 2. Multiple component discriminant model. All variables derived from the analyses of the ecological components (Table 1) were combined in a two-group discriminant analysis (across all scales and ecological components) to derive a multiple component model of the habitat of the Siskiyou Mountains salamander south of the Siskiyou Mountains crest. Standardized structure coefficients indicate the relative contribution of each variable to the discriminant function (Rencher, 1992); their signs indicate the relationship of the variable to salamander presence.

Step	Variable	*F*-Statistic	*P*	Standardized Structure Coefficient
1	Subsurface soil temp. (stand)	6.53	0.0128	0.698
2	Annual precipitation	6.62	0.0122	0.738
3	Years since disturbance	10.38	0.0020	0.399
4	% Canopy closed (plot center)	5.82	0.0186	0.692
5	Sm. decayed conifer logs_C[1]	4.40	0.0399	0.449
6	Rock_L[2]	3.27	0.0750	0.445

Wilk's Lambda = 0.595; F (df=6,65) = 7.384; P = 0.0001
Resubstitution success (%) 87.50; Cohen's Kappa = 0.4462, P = 0.0047
Jackknife success (%) = 80.56; Cohen's Kappa = 0.2525; P = 0.0670

[1] C = count per hectare
[2] L = proportion of transect line

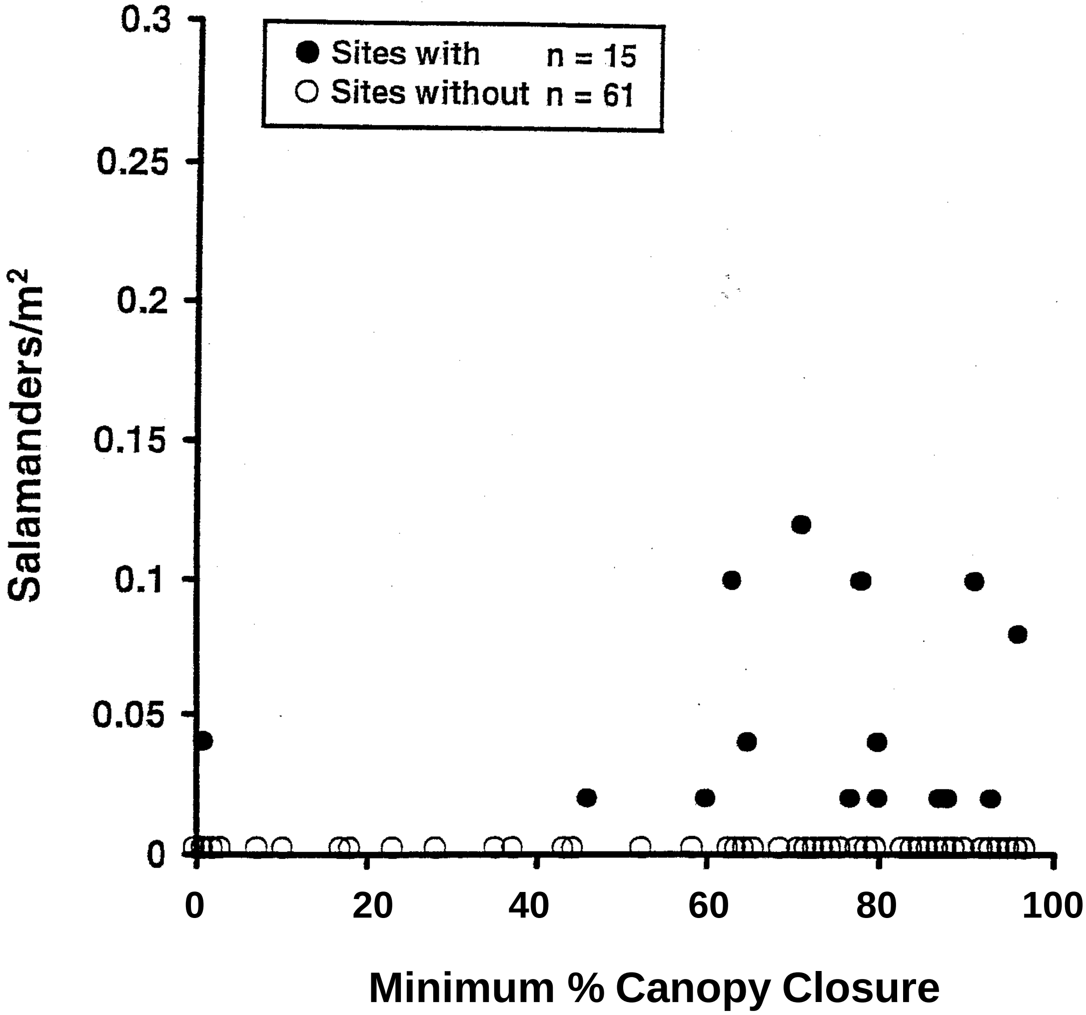


Figure 4a. Scatter plot depicting the relationship between Siskiyou Mountains salamander density and minimum canopy closure south of the Siskiyou Mountains crest.

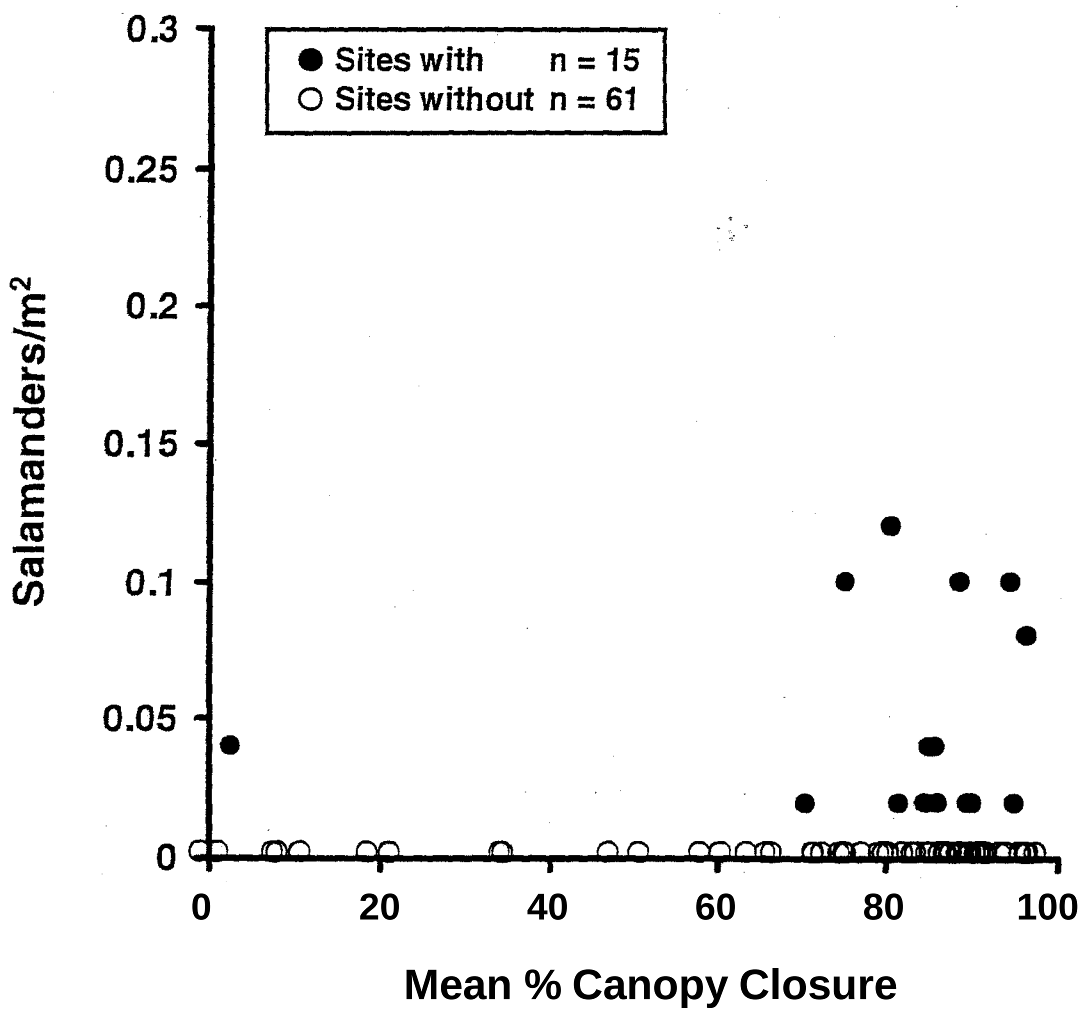


Figure 5a. Scatter plot depicting the relationship between Siskiyou Mountains salamander density and mean canopy closure south of the Siskiyou Mountains crest.

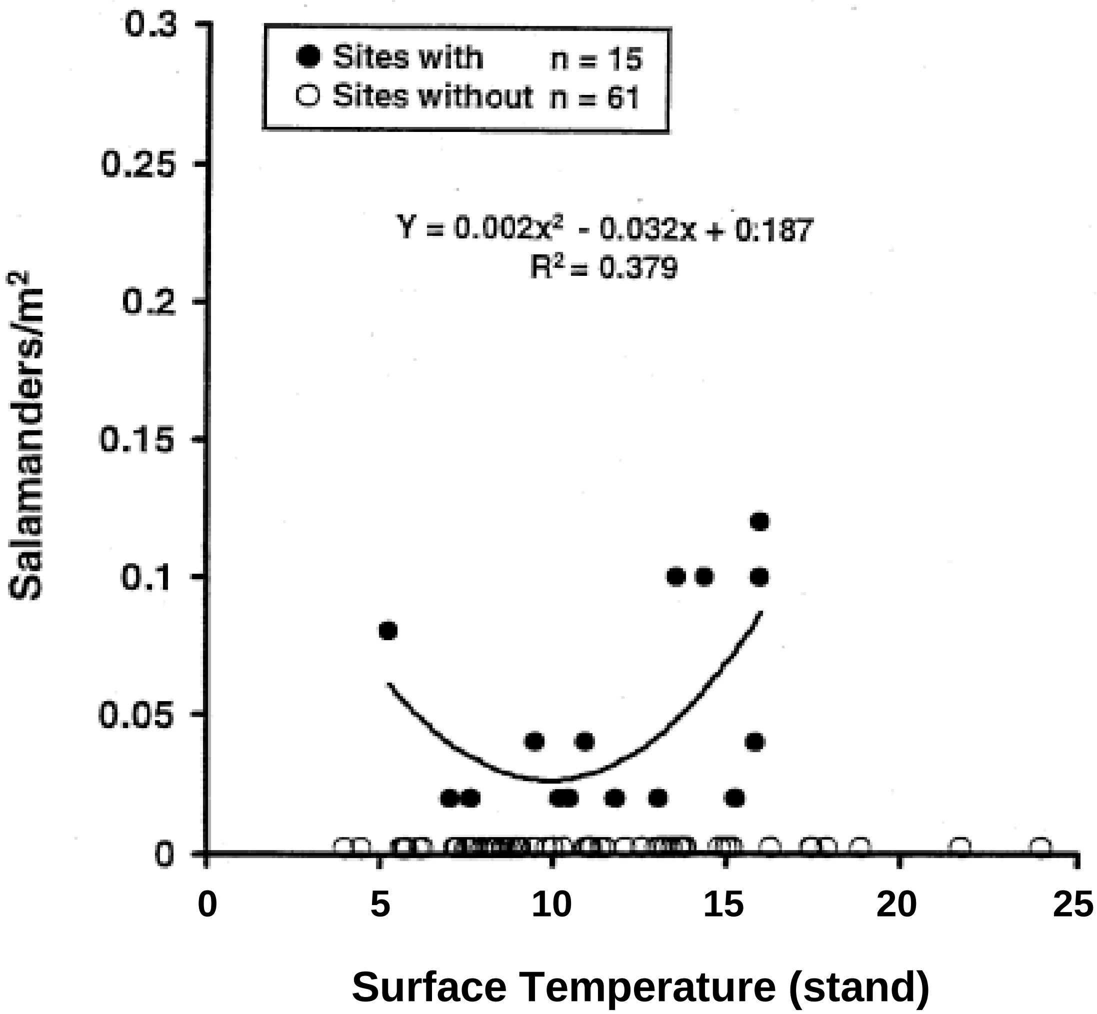


Figure 6a. Scatter plot depicting the relationship between Siskiyou Mountains salamander density and surface temperature south of the crest Siskiyou Mountains crest. The regression was calculated using sites with salamanders present only.

Oregon Sites

Discriminant Analysis.--In Oregon, longitude and aspect comprised the model that best discriminated between sites with and without salamanders at the landscape scale, indicating that sites with salamanders were more common closer to the northern portions of the range and on north facing slopes. This model discriminated between sites with and without salamanders with 66.9% accuracy, but the results were no better than chance (Table 3).

The forest structure on sites with salamanders indicated a complex structure dominated by larger conifers with a significant hardwood component (Table 3). The dead and down wood component, comprised of small decayed logs and decayed hardwood logs, indicated that sites with salamanders tended to have fewer small decayed conifer logs and more decayed hardwood logs (Table 3). Ground cover at sites with salamanders had less grass cover, more sword fern cover, more moss, deeper leaf litter, and more rock with a higher proportion of cobble-sized pieces, than did sites without animals (Table 3). All seven macrohabitat scale ecological components (Appendix. IIb) yielded models with 69% or better discriminatory power, but only five performed better than chance (Table 3).

Five of six microhabitat-scale components yielded significant models (Table 3). More understory hardwoods, sword fern, and moss distinguished between plots with and without salamanders (Table 3). The substrate model indicated that less soil, soil and sand, and more rock interstitial spaces filled with leaf litter distinguish between plots with and without salamanders (Table 3). These models had reclassification successes greater than 68%, but only two performed better than chance (Table 3).

The final composite model for the Oregon sites was comprised of variables from five

Table 3. Results of our two-group stepwise discriminant analyses of 163 sites[1] sampled for the Siskiyou Mountains salamander (*Plethodon stormi*) north of the Siskiyou Mountains crest (Oregon). Independent variables were grouped for separate analyses by ecological component (Appendix II b). Models were tested for classification success (% correct) with a jackknife procedure; *P* values indicate the significance of each model; Cohen's Kappa statistics (Titus et al., 1984) indicate the classification success of each model compared with chance.

Scale	Model variable(s)	Model score %	Model score *P*	Cohen's Kappa	Mean greater for sites with salamanders
Landscape:	Longitude	66.87	0.0071	-0.590	yes
	Aspect				no
Macrohabitat:	Hardwood trees_C[2]*	67.48	0.0025	-0.0475	yes
	All large conifers_C				yes
	Small conifer basal Area				no
	Avg. conifer diameter*	70.55	0.0223	0.0587	yes
	Sm. decayed conifer logs	69.33	0.0130	0.0436	no
	Decayed hardwood Logs				yes
	Poison oak *	69.94	0.0937	-1.34×10^{-16}	no
	Grass_L[2],*	73.01	0.0001	0.2223	no
	Sword fern_L				yes

[1] Missing values for 1 site resulted in a sample size of 162 for the calculation of the ground cover model at the macrohabitat scale.
[2] C = count per hectare, L= proportion of transect line, V = visual estimate (%) 1/10 ha circle, AV = visual estimate (%) of salamander search area.
* Indicates a model with heterogeneous variance-covariance matrices.

Table 3. (continued)

Macrohabitat (cont.):	Moss_V^{2,}*	70.99	0.0001	0.1969	yes
	Leaf litter_L				yes
	Rock_L				yes
	Cobble_V				yes
	Relative humidity	69.94	0.0073	0.0611	yes
	Solar index				no
Microhabitat:	Understory hardwoods_L	69.33	0.0314	0.0039	yes
	Sword fern_L *	68.10	0.0036	-0.0040	yes
	Moss_L	69.94	0.0607	$-1.35x10^{-16}$	yes
	Soil_AV ^{2,}*	69.94	0.0029	$-1.35x10^{-16}$	no
	Soil and Sand_AV				no
	Rock_L				yes
	Interstitial spaces avg._C (leaf litter fill)*	69.33	0.0334	0.0195	yes

ecological components, with seven variables entering in the following order: sword fern cover, grass cover, small conifer basal area, exposed cobble, moss cover, leaf litter cover, and decayed hardwood logs (Table 4). This model had a jackknife classification success of 76.5%, which was 38.4% better than random chance, and a resubstitution success of 77.2%, 40% better than chance (Table 4).

Regression Analysis. --The univariate analyses of stand level variables based on the DA yielded a significant relationship between minimum canopy closure and salamander numbers. The majority of sites with salamanders had over 60% closed canopy, with a mean of 77.8% (95% confidence interval = 71.2-84.5%)(Fig. 4b; $R^2 = 0.117$). Mean canopy closure was slightly more informative, with most sites with salamanders having greater than 70% closed canopy (Fig. 5b; $R^2 = 0.126$). However, in contrast to the California sites (Fig. 6a), the variable surface temperature at Oregon sites did not show a significant relationship with salamander numbers (Fig. 6b).

The five best multiple regression models for Oregon sites all showed increased numbers of Siskiyou Mountains salamanders with increasing hardwood tree count and increasing average diameter of conifers (Table 5). Relative humidity was higher and amounts of bare soil were lower, on sites with more animals in four of the five best models (Table 5). Greater moss cover (two models) and lower sword fern cover also entered in several of the best models (Table 5). While sword ferns indicated salamander presence (Table 3), the amount of this plant at a site varied negatively with salamander density (Table 5). This may be an artifact of our low sample sizes.

Table 4. Multiple component discriminant model. All variables derived from the analyses of the ecological components (Table 3) were combined in a two-group discriminant analysis (across all scales and ecological components) to derive a multiple component model of the habitat of the Siskiyou Mountains salamander north of the Siskiyou Mountains crest. Standardized structure coefficients indicate the relative contribution of each variable to the discriminant function (Rencher, 1992), their signs indicate the relationship of the variable to salamander presence.

Step	Variable	*F*-Statistic	*P*	Standardized Structure Coefficient
1	Sword fern (stand)	13.266	0.0004	0.483
2	Grass (stand)	7.649	0.0064	-0.328
3	All small conifer basal area	8.358	0.0044	-0.247
4	Cobble_V[1]	5.632	0.0189	0.267
5	Moss_V	6.333	0.0129	0.376
6	Leaf litter (stand)	7.385	0.0074	0.087
7	Decayed hardwood logs	4.375	0.0382	0.223

Wilk's Lambda = 0.715; F (df=7,148) = 8.574; *P* = 0.0001
Resubstitution success (%) = 77.16; Cohen's Kappa = 0.404; *P* = 0.00002
Jackknife success (%) = 76.54; Cohen's Kappa = 0.384; *P* = 0.00005

[1] V = visual estimate (%) 1/10 ha circle

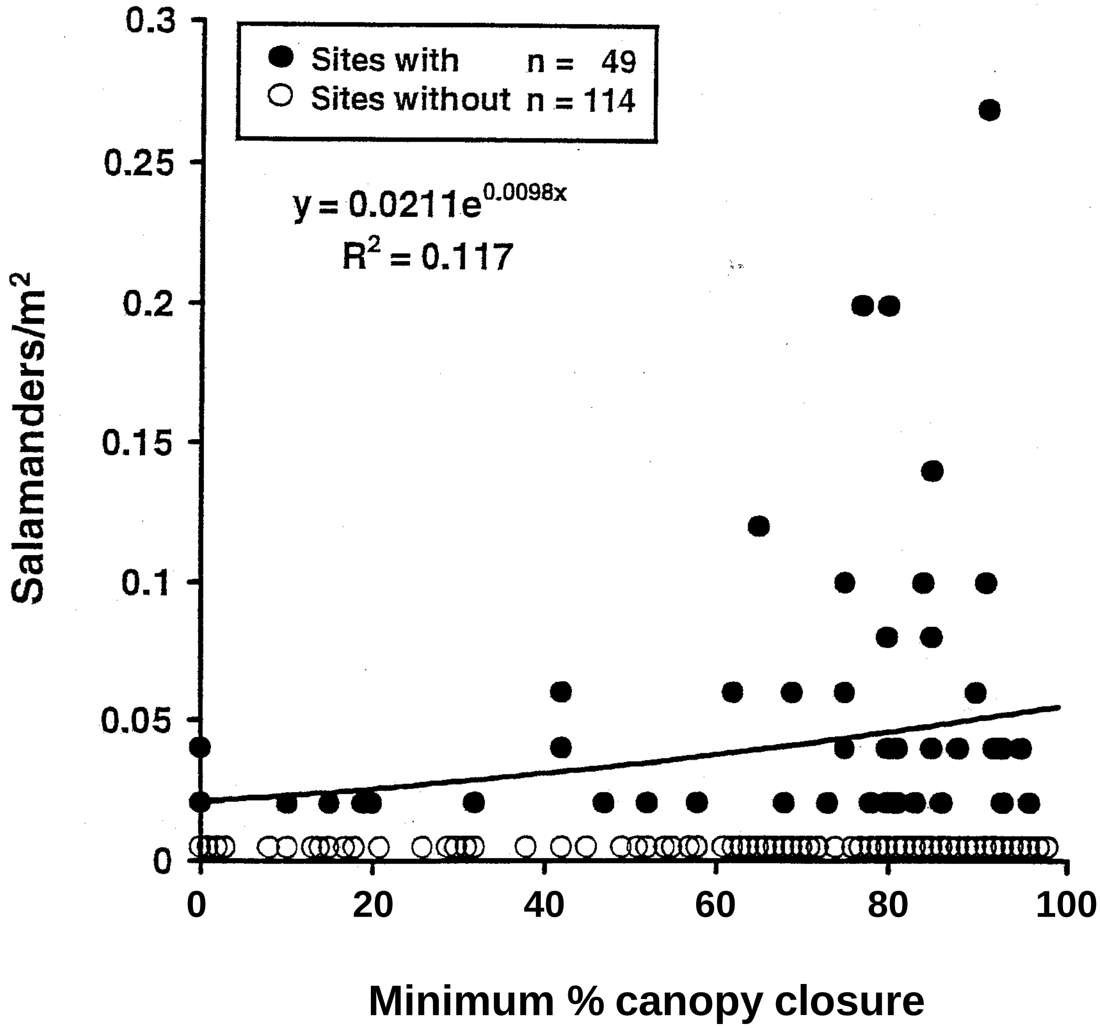


Figure 4b. Scatter plot depicting the relationship between Siskiyou Mountains salamander density and minimum canopy closure north of the Siskiyou Mountains crest. The regression was calculated using sites with salamanders present only.

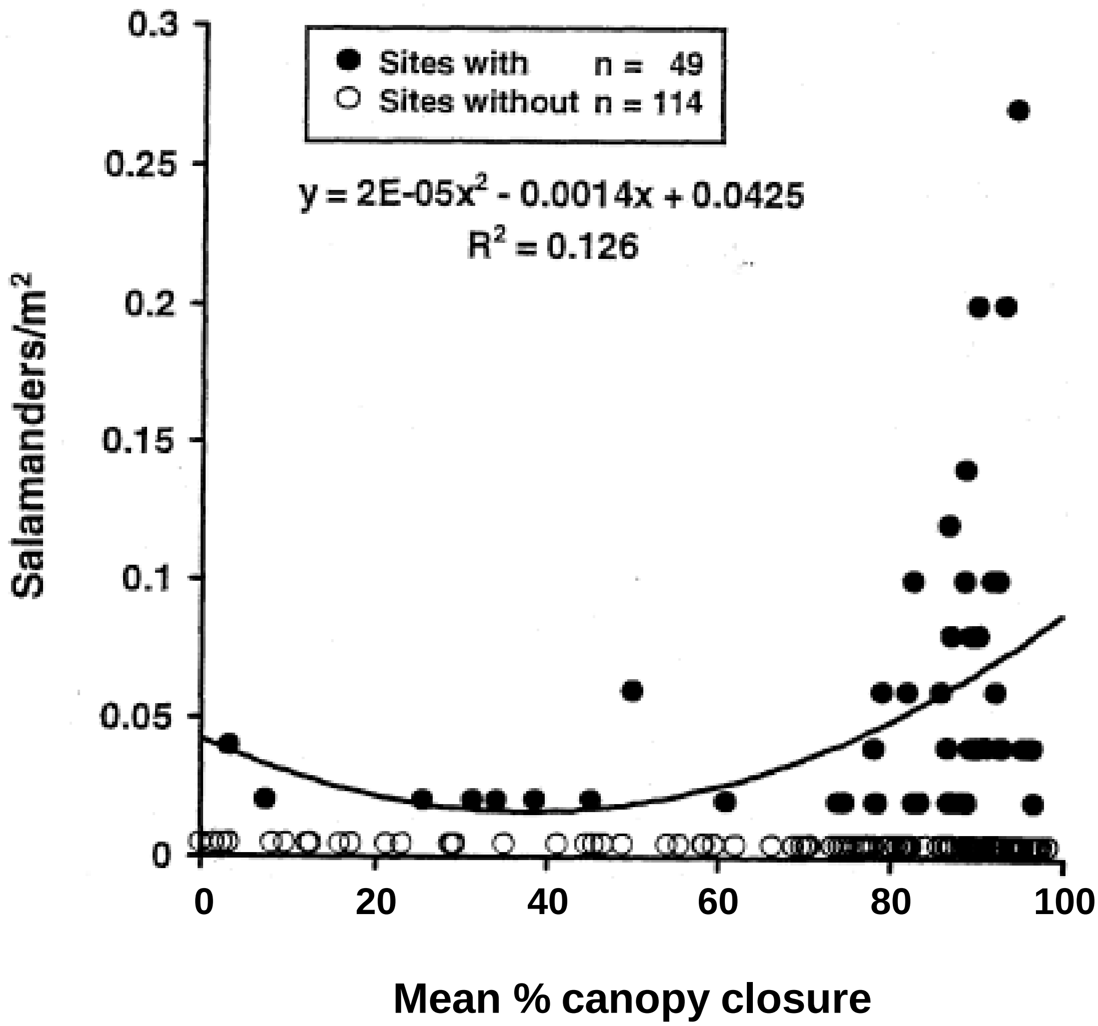


Figure 5b. Scatter plot depicting the relationship between Siskiyou Mountains salamander density and mean canopy closure north of the Siskiyou Mountains crest. The regression was calculated using sites with salamanders present only.

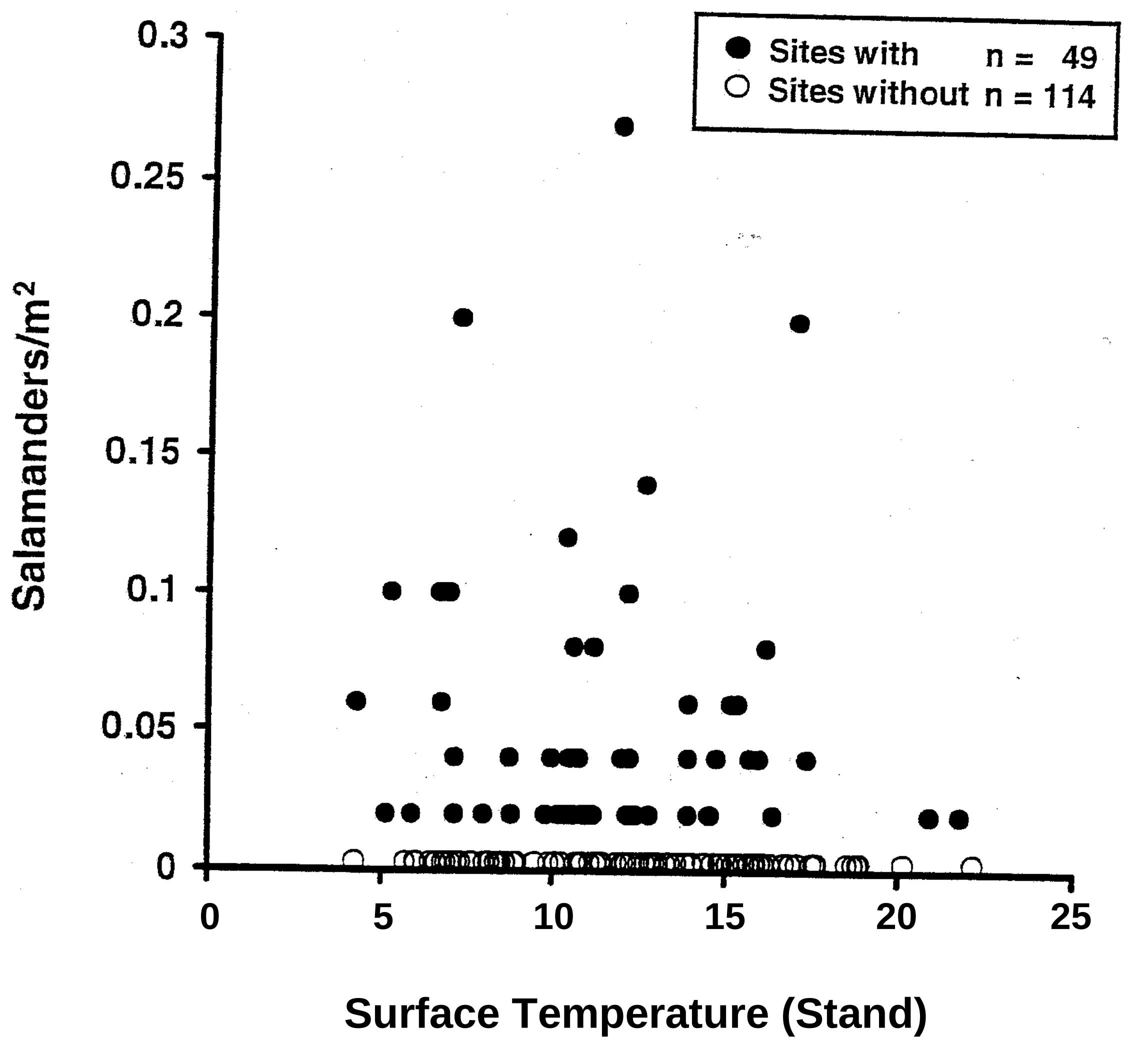


Figure 6b. Scatter plot depicting the relationship between Siskiyou Mountains salamander density and surface temperature north of the crest Siskiyou Mountains crest.

Table 5. Results of an all-possible subsets regression analysis to determine the best variable or multi-variable models for predicting densities of Siskiyou Mountains salamanders (*Plethodon stormi*) north of the Siskiyou Mountains crest. The analysis was conducted on those variables that emerged from the DA (Table 3). Best models were selected based on highest adjusted R^2 and ordered based on lowest corrected (AICc) (Hilborn and Mangel 1997). Standardized coefficients indicate the relative influence of each variable in the model; the sign indicates the relationship of the variable to numbers of salamanders.

Ecological Component	Standard coefficient	R^2(adj)	AIC_c	*F*	*P*	SE^2
Hardwood trees_C[1]	0.307					
Avg. conifer diameter	0.193					
Moss_V[1]	0.208					
Relative humidity	0.201					
Sword fern_L[1]	-0.191	0.135	95.979	2.500	0.045	2.446
Hardwood trees_C	0.325					
Avg. conifer diameter	0.236					
Relative humidity	0.187					
Sword fern_L	-0.167					
Soil_AV[1]	-0.178	0.128	96.368	2.410	0.052	2.456
Aspect	-0.184					
Hardwood trees_C	0.295					
Avg. conifer diameter	0.246					
Relative humidity	0.180					
Sword fern_L	-0.248					
Soil_AV	-0.205	0.138	97.523	2.280	0.054	2.442
Hardwood trees_C	0.310					
Avg. conifer diameter	0.195					
Moss_V	0.177					
Relative humidity	0.206					
Sword fern_L	-0.205					
Soil_AV	-0.145	0.137	97.588	2.270	0.055	2.443
Aspect	-0.228					
Hardwood trees_C	0.217					
Avg. conifer diameter	0.231					
Poison oak	-0.169					
Sword fern_L	-0.249					
Soil_AV	-0.225	0.131	97.913	2.210	0.061	2.451

[1]L = proportion of transect line, V = visual estimate (%) 1/10 ha circle, AV = visual estimate (%) of salamander search area, C = counts per hectare.

DISCUSSION

Landscape Scale

We found distinct differences in those characteristics of the landscape that support Siskiyou Mountains salamander on the two sides of the Siskiyou crest. However, some of these differences may be the result of versant-particular variations in response to the same ultimate cause, the prevailing moisture regime. For example, in Oregon those sites located closer to the western edge of the species' range, and those facing more northerly aspects had a greater likelihood of salamander presence (Table 2). Whereas in California, sites at lower elevations and toward the southern portion of the range were more likely to support salamanders (Table 1). Of particular note with regard to the California sites, as opposed to those in Oregon, is the importance of average annual precipitation, which was found to be significantly greater on sites supporting salamanders. Precipitation on the north side of the Siskiyou Mountains varies less than on the south side (Appendix. III), is probably more reliable over time, and site moisture may be retained for longer periods due to the aspect of the mountain range and the direction of prevailing weather patterns (southeast to northwest). This is born out by the fact that the Oregon sites, especially those toward the west and with more northerly aspects, received more rainfall, and the rainy period was longer in duration. On the California side of the Siskiyou crest, those sites located farther from the rainshadow affect, which were those sites further from the Siskiyou crest, were lower in elevation and farther south. In the California portion of the species' range, where precipitation is less dependable, those sites with greater amounts of rainfall would be important for maintaining populations (see Feder 1983).

Vegetational differences between the two areas also contributes to differences observed in salamander detections between the California and Oregon sites. Differences in tree density and size, plant species richness, and relative numbers of drought-tolerant plant species exist, with the California sites supporting less of a shrub layer, slower growing trees, and greater prevalence of drought-resistant species such as manzanita, canyon live oak and poison oak. The plant assemblage and structure at the California sites are indicative of a warmer, drier climate and therefore, may be less suitable habitat for Siskiyou Mountains salamander then the cooler, moister Oregon sites.

The most notable difference in landscape-scale habitat models for the two versants was the addition of the years since disturbance variable in the model for the California sites (Table 1). Disturbance in all instances was related to timber harvesting activities, which was prevalent on both versants and occurs throughout the range of this salamander. The difference in the impacts of timber harvesting between the Oregon and California sites may be related to differences in precipitation across the two versants. Two proximate, versant-specific, and microclimate-affecting conditions may contribute to the differences observed: 1) sites in the northern portion of the range had greater qualities of rocky substrates (Appendix. III); and 2) more sites with salamanders were located on north-facing aspects where microclimate fluctuations would be less severe subsequent to canopy removal from timber harvesting. Furthermore, greater soil moisture on these northern sites would allow relatively quicker regeneration of the understory and shrub layer following timber harvesting, further buffering microclimate.

The condition of the landscape as a mosaic of varyingly suitable habitats and the relationship between those habitats and the prevailing weather, determines -the various microclimates available to organisms which inhabit a landscape (Chen et al. 1999). The length of time that equable surface microclimatic conditions are within the tolerance limits of terrestrial salamanders is probably the single most important aspect of their biology, because it can affect both the density of individuals within a site and the density of occupied sites on the landscape (see Welsh and Droege 2001). Shortened periods of surface conditions appropriate for feeding and breeding activities can limit both survivorship and recruitment. Like the Del Norte salamander (Ollivier, unpubl. data), female Siskiyou Mountains salamanders probably breed every other year or less. Females must acquire sufficient body mass and develop large fat reserves in order to yolk eggs. It is likely that salamanders living at sites with microclimatic conditions limiting the duration of surface activity will take longer to achieve the body mass and fat reserves necessary for reproduction. Most recently disturbed sites we sampled appeared to lack the microclimatic conditions necessary for persistence of the species over time.

Macrohabitat Scale

At the California sites, our best DA model was that describing forest climate, a model which indicated that sites with salamanders had lower solar radiation, greater minimum canopy closure, and greater average soil temperatures, compared to sites without salamanders (Table 1). It should be noted that all sites were sampled when soil temperatures were between 4 - 18°C, so greater temperatures here indicates those that approach this upper limit. Prior studies have demonstrated decreases in salamander occurrence above this temperature (see citations in Clayton et al. 1999). Both minimum and mean canopy closure measures were good predictors of salamander presence and abundance at California sites (Table 1; Figs. 4a and 5a). The narrow and relatively high confidence interval for mean canopy closure (68.0 -93.3%) overlaps with that of the Del Norte salamander living in interior conditions of northwestern California (Welsh and Lind 1995). However, these results indicate even less tolerance for canopy openings by the Siskiyou Mountains salamander in the southern portion of its range.

The forest climate model for the Oregon sites also indicated that sites with salamanders had lower incident solar radiation, but instead of canopy closure and soil temperature as in the California model, this model contained the variable relative humidity (Table 3). Canopy closure and other aspects of stand microclimate are highly interdependent environmental parameters (Welsh and Droege 2001). Our data indicated that mean and minimum canopy closure were not as important for Oregon salamander populations as for those in California (Fig. 4a and 5a). Canopy closure may be less important on the predominantly north-facing versant in Oregon because microclimate is less affected by direct insolation. Also the presence of greater quantities of deeply layered rock in the north compared with the south (Appendix. III), may help ameliorate the loss of overstory canopy. Other significant macrohabitat models for California related salamander presence to larger minimum Douglas-fir diameters and greater amounts of small decayed conifer logs (Table 1). While no direct relationship was found with forest age, the significance of the former model suggests that some minimum requirement for stand structure is necessary to sustain populations on these southern sites. Tree size is often directly related to a lack of disturbance; sites with larger trees tend to have more closed canopies and thus more stable microclimates. Welsh and Lind (1995) found a significant relationship with forest age for the closely related Del Norte salamander. 'They interpreted forest age as a surrogate variable that models complexly structured forests with multi-layered closed canopies and stable microclimates (Welsh and Lind 1995). Bingham and Sawyer (1991, 1992) described older forests of northwestern California as having conifer-dominated canopies with a dense sub-canopy and an understory of hardwoods. Welsh and Lind (1995) reasoned that this multi-layered canopy was important to the Del Norte salamander because it contributes to the relatively cool and stable forest floor microclimate required for surface activity by plethodontid salamanders (see Feder 1983).

Oregon sites with salamanders had a dominant canopy of large conifers, greater average conifer diameter, and a large number of hardwoods (Table 3). These sites also typically had fewer small conifers, whose presence is usually an indication of site disturbance and openings in the canopy. Welsh and Lind (1995) reported understory hardwoods as important for the Del Norte salamander. They hypothesized that increased leaf fall associated with the deciduous vegetation may support a more abundant and diverse community of forest floor insects, which are prey for plethodontid salamanders, than would a pure conifer forest.

The importance of decayed conifer logs for this species in both Oregon and California (Tables 1 and 3) contrasts with that reported for the Del Norte salamander (Welsh and Lind 1995; but see Welsh and Lind 1991). While Siskiyou Mountains salamanders are not reported to use downed woody debris for cover or as refugia during periods of inhospitable climatic conditions, it may occasionally be used as cover when it occurs in conjunction with rocky substrates. In addition, it is possible that a portion of Siskiyou Mountains salamanders' prey base consists of invertebrates associated with downed wood decomposition. The presence of downed wood at sites with salamanders may also indicate greater tree density and higher soil moisture at these sites.

The ground cover models for both areas related higher levels of rock or cobble and lower levels of intermixed gravel (California only) in the stand with salamander presence (Tables 1 and 3). Greater amounts of rock in the stand provide refugia for salamanders (Herrington 1988, Nussbaum et al. 1983, Clayton et al. 1999). However, available rock must be of sizes large enough to provide interstitial access and cover. Gravel sized rock (16-32 mm diam) maybe present in a stand, but can compromise habitat quality by filling spaces between larger rocks and thus eliminating suitable microhabitat structure. The deep litter layer typical of sites with salamanders in both areas provides microclimate buffering to the rocky subsurface refugia, and it probably also supports more invertebrate prey for the salamanders. The moss layer found at the Oregon sites is probably indicative of higher, more dependable site moisture, and less ground disturbance compared to California sites. Oregon sites with salamanders also contained more decayed hardwood logs but fewer small decayed conifer logs compared to California (compare Tables 1 and 3). Hardwoods may play a more important role at Oregon sites, perhaps because they are less common there compared with the drier California sites. The shrub and understory layers did not enter models in California (Table 1), which may be due to drier conditions in this portion of the range. California sites with salamanders had fewer ferns than sites without salamanders. This variable included all fern species other than sword fern. However, in California it was typically comprised of mostly bracken fern (*Pteridium aquilinum*), which is found in open areas under more xeric conditions, often in close association with grass.

Microhabitat scale

The habitat model for sites with salamanders in California at this finest scale of resolution indicated that rocky substrates in closed-canopy forests with relatively higher soil temperatures were important (Table 1). The Oregon microsite model was similar, but added available substrate and attendant interstitial spaces as important components (Table 3). Sites with salamanders tended to have large amounts of rock, particularly in the search area, and little mineral soil and sand which can fill interstitial spaces and reduce salamander access to subterranean refugia. Leaf litter, woody debris, and moss represented additional cover available to salamanders in Oregon. A larger number of rock-associated interstitial spaces with leaf litter at a site also increased the likelihood that a site contained salamanders. Ground cover and understory composition at the California sites was very similar to the ground level model for the Oregon sites (Table 3). This salamander does not dig burrows for itself so limiting ground disturbance is crucial to maintaining access to subterranean refugia. Sites containing large amounts of relatively undisturbed, layered rocks usually yielded the highest numbers of captures per unit effort for this species (Lisa Ollivier, pers, obs.). Maiorana (1978) presented evidence of the importance of subterranean retreat space in regulating numbers in other plethodontid salamander species.

CONCLUSIONS

Across spatial scales, those variables that either directly or indirectly modeled microclimatic conditions were the best predictors of salamander presence and abundance. The habitat models for Oregon and California taken collectively indicate the importance of closed canopied, moist, relatively cool forest stands capable of supporting stable microclimates (see Chen et al. 1999). The physiological sensitivity of these salamanders and the timing of critical aspects of their life history, such as courtship, breeding, and feeding, which require surface activity, limit these behaviors to a relatively narrow climatic window (Feder 1983, Verrell 1989, Welsh and Droege 2001). Salamanders move vertically through the substrate in response to climatic charges. The presence or absence of suitable surface microclimatic regimes best explains the variation in their vertical distribution (Taub 1961). However, the proportion of a given salamander population at or near the surface at a given time is not known for any plethodontid species (Scott and Ramotnick 1992). We also do not know how long a population may remain viable if surface climatic conditions are not amenable and all individuals have to remain subsurface to avoid physiological stress.

Because of the relative rareness of the Siskiyou Mountains salamander our sample sizes were small which possibly limited the ability of our analyses to reveal and uniformly demonstrate strong relationships. For example, while most regression models were statistically significant, the regression coefficients were relatively low (Table 5) because the number of sites with captures was also low (30%) and the differences in the numbers of animals at these sites were low (1-13), both of which limited our ability to detect and demonstrate strong environmental relationships.

Nonetheless, our habitat analyses from both versants of the *P. stormi* range indicated strong relationships with aspects of mature forests such as large tree diameters, closed canopies, stable microclimates, and less disturbance. In Oregon, a dense understory and ground cover layer containing moss were additional important site characteristics. Thus, we consider this salamander to be a mature to old-growth forest-associated species that exists at its biological optimum under conditions found primarily in later seral stages of mixed conifer-hardwood forests in northwestern California and southwestern Oregon. It is important to use caution when interpreting correlative studies in the absence of accompanying data that demonstrate a cause and effect relationship. However, we believe that our study clearly links this salamander species with conditions that are found more consistently and reliably in later successional forests. This work therefore demonstrates an ecological dependence (Ruggiero et al. 1988) by the Siskiyou Mountains salamander on attributes and conditions found primarily in these mature to late seral forests. Many of the biotic and abiotic requirements necessary for long-term viability for the Siskiyou Mountains salamander remain undetermined, however this viability is clearly tied to having mature forests well-distributed and interconnected across the landscape within its' range.

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Appendix I. Variables measured during sampling for Siskiyou Mountains salamander, *Plethodon stormi*, at random sites in northern California. and southern Oregon.

Animal sample sites consisted of a 49 m^2 of surface substrate with approximately 25% rock. The 1/5 and 1/10 ha vegetation circles were placed with the sample site at or near the center; four 10 m line transects were placed at the boundary of the inner circle at random points set by a wrist watch seconds hand, the fifth 10 m transect line crosses the plot center on the original 50 m line.

<u>General site characteristics: 13 variables</u>

Elevation (m): estimated from USGS topographic maps.
Slope (percent): measured with a clinometer across the search area.
Aspect: measured with a compass, to determine the direction the search area is facing.
Township, Range and section of site.
Years since last major disturbance, note disturbance type also.
Land type - Applegate GIS geology, soil, timber classification of site.
Wildlife Habitat Relationships type

- Management type - type of timber management employed at site, or state no management.
- Removal method - how logs were removed form site
- Site preparation code - how was site prepared for replanting.
- % canopy open: measured by spherical densiometer (concave type) at 4 soil stations on the 1/10 ha circle and averaged; the open taken at the plot center is held separate.
- Air temperature (°C): measured with a thermometer at the search site, at the time of the salamander search.
- Relative humidity (%): measured with a sling psychrometer at the search site at the time of the salamander search.
- Weather: recorded at the time of the salamander search.
  - Sky = Clear, Partly cloudy, Very cloudy
  - Moisture = Dry, Foggy, Intermittent rain, Light rain, Heavy rain
  - Wind = None, Light, Moderate, Strong

<u>Tree counts and forest age (1/10 ha. 1/5 ha circles): 36 variables</u>

Trees are counted by species/type and grouped by size class (DBH).

Species/type include: ABSP (true fir species), PISP (pine species), PSME (Douglas-fir), CONF (all other conifer)species), QUCH (canyon- live oak), QUGA (Oregon white oak), and HDWD (all other hardwoods).

Small trees: Class 1 (12-26.9 cm dbh) and Class 2 (27-52.9 cm dbh) are counted in the 35.6m, diameter circle (1/10 ha). Large trees: Class 3 (53-89.9 cm dbh), Class 4 (90-119.9 cm dbh) and Class 5 (120+ cm dbh) are counted in the 50m diameter circle (1/5 ha).

Forest age will be measured using tree core data from three canopy size conifer trees of the dominant size class. The trees will be cored, aged and the mean value will be used to age the site. Three trees are to be selected within the 115 ha circle spaced around the search area.

Basal area of site: 7 variables

Basal area will be measured for the large trees within the 1/5 ha circle, small trees are measured only within the 1/10 ha circle. Each tree DBH is listed by species group on the back of the tree count form.Basal area will be calculated using BA tables in the lab. Measurements of BA will be reported as cm^2/ha.

Log, Snag and Stump counts (1/5 ha circle): 18 variables

Snags and stumps are counted within the 50m circle. Snags must be > 12 cm dbh to be counted.

Logs are counted by CONF/HDWD, size (small, large), and decay class (sound, decayed). Small logs are < 50 cm mean diameter, large logs are ≥ 50cm mean diameter; both size classes are irrespective of length. Logs must be > 10 cm diameter to be counted.

Talus and rock type: 2 variables

Record a number code for rock type (slate, chert, serpentine, etc.) and number code for talus type (sheet, rubble, mixed). These are recorded for the 1/10 ha circle.

Ground and understory cover (1/10 ha circle): 7 variables

Visual estimates of % cover within the 1/10 ha circle using the following cover types:

The following 3 types must add up to 100% cover.

- exposed mineral soil
- leaf litter
- exposed rock (also broken down into gravel, pebble, cobble, boulder).

Ten meter line transects: 28 variables

There are four 10 m line transects equidistant on the boundary of the 1/10 ha circle and one across the plot center along the original 50 m tape used for describing the circular plot. All variables are recorded as length of line covered to the nearest 1/10m, and will later be converted to %. Tree species are included on the line transect only if they are less than 12 cm dbh (too small for tree counts). Trees will be classified by species/type: true firs, Pine species, Douglas-fir, all other conifers, Canyon live oak, Oregon white oak, or all other hardwoods, etc. Other woody vegetation will be: Manzanita species, Oregon grape, Buckbrush, hazelnut, honeysuckle species, snowberry species, poison oak, sword fern, small shrubs (<2 m), and large shrubs (>2 m). Other variables are: exposed soil, rock, leaf litter, moss, lichen, grass, herb, fern, large woody debris, stream/seep, and tree bole.

Soil and litter: 9 variables

These variables will be measured at 5 points on the 1/10 ha circle and the mean value will be used to characterize the site. Measures taken at the plot center soil site will be held separate from these four.

Litter depth - measured to the nearest cm.

Soil teperature - C° at surface and at 10 cm depth.

Appendix I (cont'd)

Search area variables (49m^2 sites): 21 variables

Substrate composition: visual estimates (%) using the following categories

- Mineral soil
- Detritus Sand (0.06-2.0 mm)
- Gravel (2.0-32.0 mm)
- Pebble (32.0-64.0 mm)
- Cobble (64.0-256.0 mm)
- Boulder (256.0 + mm)
- Bedrock
- Lg. woody debris
- Leaf litter

Search time: measured in minutes.

Interstitial spaces: assigned a number code (0 = empty, 1 = soil filler, 2 = leaf litter filled, 3 = mixed leaf litter and soil). A count will be made of the number of surfaces within each of 10 equal sized planes on the vertical wall of the trench.

Capture information: 11 variables

Variables are recorded with all captures, escaped animals only have species and position data.

- Species - four letter code
- Position - relative to the substrate 0 = unknown, 1 = On, 2 = In
- Substrate - number code (see code sheet)
- Cover type - number code
- Cover size - smallest diameter in mm if a rock or log
- Life stage -1 = juvenile, 2 = subadult, 3 = adult
- Snout-vent length - measured from tip of snout to anterior vent edge (cm)
- Total length - measured from tip of snout to tip of tail (cm)
- Weight - (grams; optional measure)
- Tail autonomy- number code

Appendix IIa. Hierarchical arrangement of ecological components represented by 92 measurements of the forest environment taken in conjunction with sampling for the Siskiyou Mountains salamander (*Plethodoh stormi*) in California 1994-1998. See Appendix I for details on methods used to measure or estimate variables.

I. Landscape scale

A. Geographic relationships

- Latitude
- Longitude
- Elevation
- Slope (%)
- Aspect
- *Years since disturbance
- Annual precipitation (cm)

II. Macrohabitat or Stand Scale

A. Trees: density by size and basal area

- Forest age
- Small conifers (all)_C[2,4]
- *Small hardwoods (all)_C[3]
- Large conifers (all)_C
- Small conifers (all)_B[2]
- Large conifers (all)_B
- Small hardwoods (all)_B
- Large hardwoods (all)_B

B. Trees: variation in size

- Douglas fir
  - - mean
  - - *minimum
  - - maximum
- All pine
  - - mean
  - - minimum
  - - maximum
- All conifers
  - - mean
  - - standard deviation
- All hardwoods
  - - mean
  - - standard deviation

C. Dead and down wood: size and counts

- *Snags_C
- *Stumps_C
- *Hardwood -all logs_C
- *Conifer logs-large decayed_C
- *Conifer logs-small decayed_C
- *Conifer logs-small sound_C
- *Conifer logs-all sound_C
- *Logs_L[2]

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[1] Spatial scales arranged in descending order from coarse to fine resolution (see Wiens 1989).

[2] C = count per hectare, L = proportion of transect line, V = visual estimate (%) 1/10 ha circle, AV = visual estimate (%) of salamander search area, B = basal area per hectare.

[3] These species include W. red cedar, Incense cedar, Yew, Douglas-fir, and all pine species.

[4] These species include Madrone, Bigleaf Maple, Dogwood, California Black Oak, Chinquapin, Canyon live oak, and Oregon white oak.

* Variable was transformed for statistical analyses.

Appendix IIa. (continued)

II. Macrohabitat Scale (continued)

D. Shrub and understory composition	E. Ground-level vegetation (< .5 m)	F. Ground cover
Understry conifer (all)_L	*Fern (all)_L	Moss_L
*Understry hardwood (all)_L	*Herb_L	Lichen_L
*Poison oak_L	*Grass_V	Leaf litter_V
*Large shrub (all)_L	Height I - ground veg._V	*Exposed soil_V
*Bole_L	Small shrub (all)_L	Exposed rock_L
Height II- ground veg. _V[2]		*Gravel_V
		*Pebble_V
		Cobble_V
		*Boulder_V
		Leaf litter depth
		- mean
		- *standard deviation

II. Macrohabitat Scale (cont'd)

G. Forest climate		III. Microhabitat Scale (Animal plot) A. Shrub and understory composition (> .5 m)
Air temperature	soil temp. (surface)	*Understory conifer_L
Relative humidity	- mean.	*Understory hardwood_L
Solar index	- standard deviation	Poison oak_L
% canopy closed (stand)	soil temp. (10cm)	Large shrubs (all)_L
- minims	- mean	
- maximum	- *standard deviation	
- mean		
- standard deviation		

Appendix IIa. (continued)

III. Microhabitat Scale (continued)

B. Ground-level vegetation (< .5 m)	C. Ground cover	D. Rocky substrates
Fern (all)_L	Moss_L	*Soil and sand_AV
*Herb_L	*Lichen L	Gravel_AV
*Grass_L	Leaf litter_AV[2]	Pebble_AV
*Small shrubs (all)_L	*Logs_AV	Cobble_AV
	*Leaf litter depth	*Boulder_AV

E. Subsurface conditions	F. Microsite conditions
Interstitial spaces count by fill type (soil or mixed)	% Canopy closed (plot center)
	Soil temp. (surface)
Interstitial spaces mean count by fill type (soil or mixed)	Soil temp. (10 cm)
	*Number of *Ensatina eschscholtzii*

Appendix IIb. Hierarchical arrangement of ecological components represented by 117 measurements of the forest environment taken in conjucation with sampling for the Siskiyou Mountains salamander (*Plethodon stormi*) in Oregon 1994-1998. See Appendix I for details on methods used to measure or estimate variables.

I. Landscape scale	II. Macrohabitat or Stand Scale	
A. <u>Geographic relationships</u>	A. <u>Trees: density by size and basal area</u>	B. <u>Trees: variation in size</u>
Latitude	Forest age	Douglas-fir
Longitude	*Small Douglas-fir_C	- mean
*Elevation	Large Douglas-fir_C[2]	- *minimum
Slope (%)	Canyon live oak_C	- maximum
Aspect	*All pine species_C	Canyon live oak
*Years since disturbance	Other hardwoods_C[3]	- mean
Annual precipitation (cm)	Small conifers (all)_C[4]	- minimum
	Large conifers (all)_C	- maximum
	*Hardwoods (all)_C	All conifers[4]
	Small Douglas-fir_B	- mean
	Large Douglas-fir_B	- standard deviation
	Canyon live oak_B	Other hardwoods[3]
	Small conifers (all)_B	- mean
	Large conifers (all)_B	- standard deviation
	*Hardwoods (all)_B[5]	

[1] Spatial scales arranged in descending order from coarse to fine resolution (see aliens 1989).
[2] C = count per hectare, B = basal area per hectare, L= proportion of transect line, V = visual estimate (%) 1/10 ha circle, AV = visual estimate (%) of salamander search area. .
[3] These species include Madrone, Bigleaf Maple, Dogwood, California Black Oak, Chinquapin.
[4] These species include W. red cedar, Incense cedar, Yew, Douglas-fir, and all pine species.
[5] These species include Madrone, Bigleaf Maple, Dogwood, California Black Oak, Chinquapin, Canyon live oak, and Oregon white oak.
* Variable was transformed for statistical analyses.

Appendix IIb. (continued)

II. Macrohabitat or Stand Scale (continued)

C. Dead and down wood: size anal counts

*Snags_C	*Conifer logs- sound_C
Stumps_C	*Hardwood logs-decayed_C
*Conifer logs-small decayed_C	*Hardwood logs-all_C
*Conifer logs-large decayed_C	*Logs_L[2]

II. Macrohabitat Scale (cont'd)

D. Shrub and Understory Composition (>0.5 m)	E. Ground-level Vegetation (<0.5 m)
Bole_L	*Fem_V
*Understory Douglas-fir_L	*Grass_L
*Understory Canyon live oak_L	*Herb_L
*Understory conifers (all)_L	Height I - ground veg._V
*Understory hardwoods (all)_L	*Sword fern_L
Hazelnut_L	*Oregon grape_L
Poison oak_L	*Honeysuckle_L
*Other large shrubs_L	*Snowberry_L
Height II - vegetation_V[8]	*Other small shrubs_L

II. Macrohabitat Scale (cont'd)

F. Ground cover

Moss_V

*Lichen_V

Leaf litter_L

*Exposed soil_V

Exposed rock_L

Gravel_V

Pebble_Y

Cobble_V

Boulder_V

Leaf litter depth

- mean.
- *standard deviation

G. Forest climate

Air temperature

Relative humidity

Solar index

% canopy closed (stand)

- minimum
- maximum
- mean
- *standard deviation

Soil temp. (surface)

- mean
- *standard deviation

Soil temp. (10cm)

- mean
- *standard deviation

III. Microhabitat Scale (Animal plot)

A. Shrub and understory composition (> .5 m)

*Understy Douglas-fir_L

*Understy Canyon live oak_L

*Understory conifers (all)_L

*Understory hardwoods (all)_L

*Poison oak_L

*Large shrubs (all)_L

B. Ground-level vegetation (< .5 m)

*Fern (all)_L

*Herb L

*Grass L

*Oregon grape_L

*Sword fern_L

*Honeysuckie_L

Snowberry_L

*Small shrubs (all) _L

C. Ground cover

Moss_L

*Lichen_L

Leaf litter_L

*Logs_AV[8]

Leaf litter depth

D. Rocky substrates

*Soil_AV

*Soil and sand_AV

*Gravel_AV

Pebble_AV

Cobble_AV

*Boulder_AV

*Large rock_AV

*Rock_L

Appendix IIb. (continued)

III. Microhabitat Scale - (cont'd)

E. Subsurface conditions	F. Microsite conditions
Interstitial spaces count by fill type (soil*, leaf litter, mixed)	% Canopy closed (plot center)
	Soil temp. (surface)
Interstitial spaces mean count by (soil, leaf litter, mixed) fill type	Soil temp. (10 cm)
	*Number of *Ensatina eschscholtzii*

Appendix. III. Descriptive statistics for sites sampled for Siskiyou Mountains salamanders both north and south of the Siskiyou Mountains crest. Statistics are calculated for sites with (a) and without (b) salamanders.

a).

Measure	units	State	n	mean	standard error	minimum	maximum	95% CT
Annual precipitation	cm	South	15	122.43	10.12	63.50	195.58	100.72 - 144.14
	cm	North	49	92.63	3.06	68.58	154.94	86.48 - 98.78
Canopy closure	%	South	15	80.65	5.88	2.75	96.50	68.03 - 93.26
(Stand)	%	North	49	77.88	3.30	4	97.5	71.24 - 84.52
Canopy closure	%	South	15	79.87	6.08	2	99	66.83 - 92.91
(Plot center)	%	North	49	76.83	3.75	0	98	69.29 - 84.37
Exposed soil	%	South	15	3.47	0.86	0	10	1.63 - 5.31
(Stand)	%	North	49	3.22	0.63	0	25	1.95 - 4.49
Rock (stand)	prop.	South	15	0.49	0.09	0.07	1.00	0.30 - 0.68
	prop.	North	49	0.75	0.03	0.31	1.00	0.69 - 0.81
Rock	prop.	South	15	0.58	0.07	0.18	1.00	0.43 - 0.73
(plot center)	prop.	North	40	0.90	0.02	0.35	1.00	0.86 - 0.94

b).

Measure	units	State	n	mean	standard error	minimum	maximum	95% CI
Annual precipitation	cm	South	61	101.56	4.33	58.42	195.58	92.90 -110.22
	cm	North	114	92.55	2.19	63.50	160.02	88.21 - 96.89
Canopy closure	%	South	61	72.64	5.88	2.75	96.50	60.88 - 84.40
(Stand)	%	North	114	73.50	2.60	0	98.5	68.35 - 78.65
Canopy closure	%	South	61	68.10	4.03	0	98	60.04 - 76.16
(Plot center)	%	North	114	69.05	2.87	0	100	63.36 - 74.74
Exposed soil	%	South	60	4.42	0.58	0	25	3.26 - 5.58
(Stand)	%	North	114	4.67	0.71	0	70	3.26 - 6.08
Rock (stand)	prop.	South	61	0.35	0.04	0	1.00	0.27 - 0.43
	prop.	North	114	0.62	0.02	0.02	1.00	0.58 - 0.66
Rock	prop.	South	61	0.62	0.04	0.09	1.00	0.56 - 0.70
(plot center)	prop.	North	114	0.78	0.03	0	1.00	0.72 - 0.84